

# Nonagricultural Hosts of *Prostephanus truncatus* (Coleoptera: Bostrichidae) in a West African Forest

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**ABSTRACT** *Prostephanus truncatus* (Horn) is an important insect pest on stored maize, *Zea mays* L., and cassava, *Manihot esculenta* Crantz, in Africa, but weekly pheromone-baited trap catches in West and East Africa exceeding 1000 individuals suggest that this insect is also well established in nonagricultural areas. The magnitude of pheromone-baited trap catches on the African continent emphasizes the importance of looking into the nonagricultural hosts of *P. truncatus*, because “wild” *P. truncatus* populations may be a threat to nearby food storage systems. In this study, we used a combination of 1) laboratory no-choice rearing tests on forest branches, roots, and seeds; 2) a behavioral experiment; 3) a review of published studies on the spatial ecology and host range of *P. truncatus*; and 4) a comparison of estimated *P. truncatus* production from potential forest hosts with the magnitude of pheromone trap catches, to discuss the possible role of different hosts in the *P. truncatus* ecology in West Africa. In no-choice tests, we evaluated the ability of *P. truncatus* to attack and reproduce on 1) fresh branches from 26 plant species, 2) dry branches from 13 species, 3) fresh roots from 18 species, 4) dry roots from two species, and 5) seeds from four species. Heavy attacks occurred on fresh branches from 11 tree species and fresh roots from four tree species. High reproductive rate was found on branches from four species and on roots from two species, and *P. truncatus* reproduction was also observed on teak, *Tectona grandis* Linn. F., seeds. We provided rough estimates of *P. truncatus* populations from different forest hosts and compared them with the spatial distribution pattern and the magnitude of pheromone-baited trap catches in a West African forest. The results from this study underscored the importance of further research into the possible role of girdled branches of *Lannea nigriflora* (Sc. Elliot) Keay (Anacardiaceae), forest seeds, and roots in the *P. truncatus* ecology in West Africa.

**KEY WORDS** Benin, forest seeds, host evaluation, stored-product pests

THE LARGER GRAIN BORER, *Prostephanus truncatus* (Horn) (Coleoptera: Bostrichidae), is a major introduced pest of stored maize, *Zea mays* L., and cassava in Africa, and it is native to Mesoamerica (Hodges 1994), where it has been known to infest stored maize for several centuries (Holst et al. 1999). Bostrichids in general live on felled timber or dead wood (Richards and Davies 1977) and *P. truncatus* is considered a wood-boring species (Nang'ayo et al. 1993, Ramírez-Martínez et al. 1994, Scholz et al. 1997) that has recently become secondarily adapted to stored commodities (Markham 1990). Chittenden (1911) wrote

that tubers and roots probably serve as the natural host for *P. truncatus*, and Li (1988) suspected that the original hosts were probably soft, starchy woods. A better understanding of the host range of *P. truncatus* is important to anticipate the ultimate range of this pest and to evaluate to what extent *P. truncatus* populations in nonagricultural environments are to be considered a threat to nearby food storage systems. Nansen and Meikle (2002) reviewed the biology of *P. truncatus* on agricultural and nonagricultural hosts and found that the nutritional biology (including the role of symbionts), host finding behavior, and the survivorship in nonagricultural environments are subjects that deserve future attention.

Thus far, the only documented forest hosts for *P. truncatus* are branches of trees in the family Anacardiaceae that have been girdled by cerambycids [Benin, Borgemeister et al. (1998); Kenya, Nang'ayo (1996); and Mexico, Ramírez-Martínez et al. (1994)]. Ramírez-Martínez et al. (1994) and Nang'ayo (1996) did not provide the number of dissected branches. Borgemeister et al. (1998) inspected two collections of 65 and 40 girdled branches of *Lannea nigriflora* (Sc.

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Elliot) Keay (Anacardiaceae) made in the Lama forest in southern Benin and found 57 and 104 *P. truncatus* individuals, respectively. Although these data confirm that *P. truncatus* is established in the Lama forest, their ecological importance is difficult to assess without quantitative data on the distribution and densities of both *L. nigritana* and *P. truncatus* in the forest.

The purpose of this study was to evaluate the importance of known *P. truncatus* hosts in nonagricultural environments and to consider other host resources as well. Based on 1) laboratory rearing tests on forest branches, roots, and seeds; 2) a behavioral experiment; 3) review of published studies on the spatial ecology and host range of *P. truncatus*; and 4) estimates of *P. truncatus* production from potential forest hosts and comparison of these estimates with the magnitude of pheromone-baited trap catches, we discuss the potential of different hosts in nonagricultural areas in West Africa.

### Materials and Methods

**Lama Forest.** Most of the forest hosts examined in this study were collected in the Lama forest in southern Benin, and data from this forest on the spatial distribution of pheromone-baited trap catches of *P. truncatus* and of trees species were used to generate population estimates of different hosts inside the forest. Thus, a brief description is provided of the size and tree species composition of the Lama forest, but more detail is available in Nansen et al. (2001). The Lama forest (6° 55.8' to 6° 58.8' N and 2° 4.2' to 2° 10.8' E) is located ≈90 km north of the coast to the south, and it covers a total area of ≈47 km<sup>2</sup> of which only 25 km<sup>2</sup> were considered undisturbed forest in 1987 (Emrich et al. 1999). In the Lama forest, average maximum daily temperatures follow a unimodal yearly pattern with a maximum around February (35°C) and minimum in August (<30°C). The mean annual rainfall in the Lama forest is ≈1,100 mm. Nansen et al. (2001) identified 32 tree species and five forest types in the Lama forest, based on a sample of 69 225-m<sup>2</sup> plots.

**Reproductive Rate of *P. truncatus* Strains.** A preliminary study was conducted to determine whether *P. truncatus* individuals from the laboratory colony at the International Institute of Tropical Agriculture (IITA) in Cotonou, Benin, could be used to assess the reproductive rate on potential forest hosts compared with wild *P. truncatus* individuals from the Lama forest. Wild *P. truncatus* individuals were obtained from five jars of whole maize (unknown local variety), each containing a *P. truncatus* pheromone lure (Agrisense-BCS, Pontypridd, UK), that were placed inside the Lama forest for 1 wk at least 700 m from nearest maize field or maize store. Groups of 20 unsexed *P. truncatus* individuals from the wild-caught and the laboratory strains were reared in no-choice tests for 2 mo under controlled conditions (30 ± 3°C and 75 ± 10% RH) at IITA on the following substrates (number of tests): whole maize kernels (unknown local variety) (5), *Ceiba pentandra* (L.) Gaertn. (Bombacaceae)

branches (30), *Delonix regia* (Bojer ex Hook.) Raf. (Fabaceae) branches (3), *Ficus exasperata* Vahl. (Moraceae) roots (2), *Ficus capensis* Thunb. (Moraceae) branches (6), and girdled branches of *L. nigritana* (2). These host materials were chosen due to prior observations about their susceptibility to attack by *P. truncatus*. We used unsexed *P. truncatus*, because an earlier study of the same laboratory strain had shown that the sex ratio was 1:1 (Vowotor et al. 1997).

**Attack Scores and Reproductive Rates.** In no-choice tests conducted under the conditions described above and with 20 unsexed *P. truncatus* individuals in each rearing test, we assessed the reproductive success of *P. truncatus* on 1) fresh branches from 26 tree species (Table 1), 2) girdled branches two species (Table 1), 3) dry branches from 13 tree species (Table 2), 4) fresh roots from 18 species (Table 3), 5) dry roots from two species (*F. capensis* and *F. exasperata*), and 6) seeds from four species: *Afzelia africana* Sm. (Fabaceae) (36 tests), *Vitellaria paradoxa* C.F. Gaertn. (Sapotaceae) (24 tests), *Elaeis guineensis* Jacq. (Arecaceae) (15 tests), and *Tectona grandis* (teak) Linn. f. (Verbenaceae) (191 tests). The tree species examined (branches, roots, and/or seeds) represented ≈64% of the trees in the Lama forest (Nansen et al. 2001). Important exceptions were *Pancovia bijuga* Willd. (Sapindaceae) and *Drypetes floribunda* (Muell. Arg.) Hutch. (Euphorbiaceae) (Nansen et al. 2001). Although *P. bijuga* and *D. floribunda* are abundant in undisturbed parts of the Lama forest and represent ≈26.3% of the trees (Nansen et al. 2001), their wood was considered too hard for attack by *P. truncatus* and they were not considered further. In addition, we examined host material from five species found in the area but not considered forest plants: *D. regia*, *Manihot esculenta* Crantz (Euphorbiaceae), *T. grandis*, *Terminalia superba* Engl. & Diels (Combretaceae), and *Anacardium occidentale* L. (Anacardiaceae). All branches and roots were collected between December 1997 and March 2000 in the Lama and the Penneselou forests (southern Benin and central Benin, respectively) by cutting samples from living and dead trees (branches on the ground were not collected). Fresh branches and roots were cut to pieces ≈4 cm in length with a diameter between 2 and 6 cm, and they were dried for up to 60 d in a closed room (25–35°C) before testing. Slow drying of branches and roots allowed us to test the same host material at different moisture contents. Moisture content was determined at the start of each rearing test from a separate piece of the same branch or root and was calculated as the percentage difference between the wet weight and the dry weight, after 24 h in an oven at 70°C.

Host pieces were examined externally after 2 wk of rearing, and an "attack score" was assigned to each piece according to the number of entry holes produced by *P. truncatus*: 0, no entry holes; 1, one or two entry holes; 2, three to five entry holes; or 3, more than five entry holes. After 2 mo of testing, the piece was dissected, and the reproductive rate of *P. truncatus* was calculated by dividing the total number of larvae,

Table 1. Moisture content, number of rearing tests, and attack scores of fresh branches tested as potential forest hosts for *P. truncatus*

Species	Family	Moisture content			Tests	Attack score			
		Mean	Min.	Max.		0	1	2	3
<i>C. pentandra</i>	Bombacaceae	38.5	10.2	68.6	554	70	159	149	176
<i>F. exasperata</i>	Moraceae	30.6	10.2	67.3	192	101	51	8	32
<i>D. regia</i>	Fabaceae	37.9	8.8	66.2	183	24	29	37	93
<i>M. esculenta</i>	Euphorbiaceae	65.3	24.7	88.1	174	13	33	59	69
<i>T. grandis</i>	Verbenaceae	32.3	11.3	55.4	108	77	27	4	0
<i>F. capensis</i>	Moraceae	30.7	11.6	63.8	105	89	12	3	1
<i>F. xanthoxylodes</i>	Rutaceae	24.0	11.2	42.5	102	60	29	11	2
<i>S. tragacantha</i>	Sterculiaceae	48.2	11.6	73.9	93	34	9	21	29
<i>G. arborea</i>	Verbenaceae	39.4	16.7	61.1	84	64	16	4	0
<i>T. superba</i>	Combretaceae	30.1	10.7	46.9	81	53	15	6	7
<i>L. sericeus</i>	Fabaceae	30.7	13.8	53.5	81	69	11	1	0
<i>L. nigritana</i>	Anacardiaceae	43.5	9.4	63.1	69	35	17	9	8
<i>H. floribunda</i>	Apocynaceae	35.2	16.0	65.3	54	50	3	1	0
<i>D. guineense</i>	Fabaceae	20.0	4.8	42.1	48	48	0	0	0
<i>A. leiocarpus</i>	Combretaceae	16.1	10.9	37.4	42	42	0	0	0
<i>P. discoideus</i>	Euphorbiaceae	20.4	10.6	47.7	42	36	5	1	0
<i>A. zygia</i>	Fabaceae	26.3	12.2	44.6	33	26	6	1	0
<i>C. africana</i>	Anacardiaceae	53.1	41.1	63.4	30	2	0	12	16
<i>K. senegalensis</i>	Meliaceae	19.5	11.3	35.0	27	27	0	0	0
<i>C. brounii</i>	Ulmaceae	19.7	9.6	35.7	24	23	1	0	0
<i>D. mespiliformis</i>	Ebenaceae	25.9	12.6	48.5	24	24	0	0	0
<i>L. cupanioides</i>	Sapindaceae	26.2	15.1	47.2	24	23	1	0	0
<i>V. colorata</i>	Asteraceae	21.8	10.9	38.2	24	21	3	0	0
<i>A. occidentale</i>	Anacardiaceae	49.2	29.2	72.2	21	20	1	0	0
<i>F. glumosa</i>	Moraceae	11.7	10.3	15.6	18	14	4	0	0
<i>V. paradoxa</i>	Sapotaceae	25.9	12.6	44.9	18	17	1	0	0
<i>L. nigritana</i> (Gird)	Anacardiaceae	46.8	36.6	56.9	6	3	0	1	2
<i>A. occidentale</i> (Gird)	Anacardiaceae	41.9	41.9	41.9	3	3	0	0	0

Results from no-choice rearing tests on fresh branches from 26 tree species. The moisture content was determined at the time the rearing test was initiated. “(Gird)” after species name means that the branches had been girdled by cerambycids. Tree species are sorted according to the number of rearing tests. Pieces of each tree species were infested with 20 unsexed *P. truncatus* adults. Most of the branches were tested at several moisture contents. “Test” denotes the total number of rearing tests for each tree species. After 2 wk of rearing, we performed a visual assessment of the number of entry holes in the host materials: 0, no entry holes; 1, one or two entry holes; 2, three to five entry holes; or 3, more than five entry holes.

pupae, and adults by the initial population. To compare the reproductive rate on potential forest hosts with that of a known substrate, we conducted 10 tests with 20 unsexed *P. truncatus* adults on 200 g of whole maize kernels under the same rearing conditions.

Seed Classes. The *P. truncatus* reproduction on forest seeds was tested under the same rearing conditions as for branches and roots, but moisture content was not determined. Six unsexed *P. truncatus* adults were reared on five to 10 seeds in each test. Dry seeds of *A.*

Table 2. Moisture content, number of rearing tests, and attack scores of dry branches tested as potential forest hosts for *P. truncatus*

Species	Family	Moisture content			No.	Attack score			
		Mean	Min.	Max.		0	1	2	3
<i>C. pentandra</i>	Bombacaceae	14.0	5.7	20.4	150	133	7	1	3
<i>D. regia</i>	Fabaceae	14.0	12.0	18.8	21	15	0	0	0
<i>F. exasperata</i>	Moraceae	14.5	12.0	16.6	18	1	1	5	5
<i>T. grandis</i>	Verbenaceae	14.8	11.7	20.0	18	10	5	2	1
<i>D. guineense</i>	Fabaceae	12.1	9.9	14.2	12	12	0	0	0
<i>F. xanthoxylodes</i>	Rutaceae	10.9	9.6	12.3	12	12	0	0	0
<i>F. capensis</i>	Moraceae	11.4	11.1	11.8	12	6	0	0	0
<i>L. sericeus</i>	Fabaceae	11.7	10.5	12.9	12	12	0	0	0
<i>T. superba</i>	Combretaceae	20.4	18.8	22.7	9	9	0	0	0
<i>L. nigritana</i> (Gird)	Anacardiaceae	11.7	11.7	11.7	6	0	0	5	1
<i>A. leiocarpus</i>	Combretaceae	11.7	11.7	11.7	6	6	0	0	0
<i>S. tragacantha</i>	Sterculiaceae	12.0	12.0	12.0	6	4	1	1	0
<i>V. colorata</i>	Asteraceae	9.5	9.5	9.5	6	6	0	0	0

Results from no-choice rearing tests on dry branches from 13 tree species. The moisture content was determined at the time the rearing test was initiated. “(Gird)” after species name means that the branches had been girdled by cerambycids. Tree species are sorted according to the number of rearing tests. Pieces of each tree species were infested with 20 unsexed *P. truncatus* adults. Most of the branches were tested at several moisture contents. “Test” denotes the total number of rearing tests for each tree species. After 2 wk of rearing, we performed a visual assessment of the number of entry holes in the host materials: 0, no entry holes; 1, one or two entry holes; 2, three to five entry holes; or 3, more than five entry holes.

Table 3. Moisture content, number of rearing tests, and attack scores of fresh roots tested as potential forest hosts for *P. truncatus*

Species	Family	Moisture content			No.	Attack score			
		Mean	Min.	Max.		0	1	2	3
<i>F. exasperata</i>	Moraceae	43.2	25.6	61.3	16	1	1	0	14
<i>F. capensis</i>	Moraceae	38.5	22.8	48.6	16	2	0	0	14
<i>S. tragacantha</i>	Sterculiaceae	62.9	60.3	66.5	12	6	0	2	4
<i>A. africana</i>	Fabaceae	36.9	27	46.4	12	8	1	3	0
<i>T. superba</i>	Combretaceae	41.2	33	50.1	12	10	0	2	0
<i>A. leiocarpus</i>	Combretaceae	20.8	15.4	25.8	12	12	0	0	0
<i>D. guineense</i>	Fabaceae	27.2	18.1	34	12	12	0	0	0
<i>D. mespiliformis</i>	Ebenaceae	32.6	23.8	37.8	12	12	0	0	0
<i>D. floribunda</i>	Euphorbiaceae	31.1	25	37.2	12	12	0	0	0
<i>G. arborea</i>	Verbenaceae	51.1	49	55.8	12	12	0	0	0
<i>H. floribunda</i>	Apocynaceae	26.3	17.8	37.7	12	12	0	0	0
<i>L. sericeus</i>	Fabaceae	35	27.7	42.2	12	12	0	0	0
<i>M. andongensis</i>	Sapotaceae	28.9	27.3	30.3	12	12	0	0	0
<i>T. grandis</i>	Verbenaceae	37.5	29.9	44.7	12	12	0	0	0
<i>F. xanthoxyloides</i>	Rutaceae	28.4	22.2	32.5	9	6	0	3	0
<i>D. regia</i>	Fabaceae	40.4	34.7	51.9	9	9	0	0	0
<i>K. senegalensis</i>	Meliaceae	31.9	28.1	35.7	9	9	0	0	0
<i>P. discoideus</i>	Euphorbiaceae	27	14.7	36.9	9	9	0	0	0

Results from no-choice rearing tests on fresh roots from 18 tree species. The moisture content was determined at the time the rearing test was initiated. “(Gird)” after species name means that the branches had been girdled by cerambycids. In tree species are sorted according to the number of rearing tests. Pieces of each tree species were infested with 20 unsexed *P. truncatus* adults. Most of the branches were tested at several moisture contents. “Test” denotes the total number of rearing tests for each tree species. After 2 wk of rearing, we performed a visual assessment of the number of entry holes in the host materials: 0, no entry holes; 1, one or two entry holes; 2, three to five entry holes; or 3, more than five entry holes.

*africana* and *E. guineensis* were collected on the ground in the Lama forest, and *V. paradoxa* seeds were collected on the ground in the Pennesselou forest. All teak seeds originated from the Lama forest and were divided into four phenological classes: 1) still attached to tree, 2) recently shed with an intact pericarp (light green or brown), 3) shed with mesocarp but lacking a pericarp, and 4) shed with a slightly decomposed mesocarp. Teak seeds in phenological classes 2–4 were collected monthly from March 1999 to March 2000, but seeds in class 1 could be collected only during the 7-mo teak fruiting period from August 1999 to February 2000. In an attempt to observe *P. truncatus* attack of teak seeds in the field, 120 seeds were collected each month, divided into six samples in separate jars (20 seeds in each jar), and examined daily for 2 mo under the laboratory conditions described above.

**Teak Seed Production.** The seed production per m<sup>2</sup> in the teak plantation of the Lama forest was estimated by counting and then removing all teak seeds in six 10 by 10-m plots once per month. Three plots were established on the eastern side and three plots on the northern side of the forest. All plots were established in the beginning of August 1999, cleared of teak seeds, and sampled during the fruiting period from August 1999 to February 2000. In southern Benin, the dry season starts around November to December, and because by February teak trees shed their leaves and remaining seeds, the seed production per year was estimated during the 7-mo fruiting period.

***P. truncatus* and the Soil Environment.** Twenty glass jars (10 cm in diameter and 15 cm in height) were filled with soil up to 1 cm from the rim, and five teak seeds (recently shed with an intact light green or brown pericarp) were buried in each jar ≈2 cm below the soil surface. Jars were placed inside a pole barn to

reduce the effects of direct sunlight and rain while allowing the beetles the opportunity to escape. We placed five unsexed *P. truncatus* <14 d old on top of the soil inside each jar. After 48 h, the *P. truncatus* individuals were described as 1) walking on the soil surface, 2) dead on the soil surface, 3) burrowing into the soil, 4) dead in the soil, 5) alive in teak seeds, 6) dead in teak seeds, and 7) flown (not found in the jars).

**Statistical Analyses.** PROC MIXED, SAS 8.01 (SAS Institute 1999) was used to examine the difference in reproductive rate of *P. truncatus* caught with traps in the forest and from the IITA laboratory strain. PROC MIXED with contrasts was used to examine the means of moisture content of fresh branches of *C. pentandra*, *D. regia*, *F. exasperata*, and *M. esculenta* in rearing tests with different attack scores. PROC NLIN was used to analyze moisture content as an explanatory variable of the reproductive rate of *P. truncatus* on six host materials: fresh branches of *C. pentandra*, *D. regia*, *F. exasperata*, and *M. esculenta*, fresh roots of *F. exasperata* and *F. capensis*. The following equation, adapted from Meikle et al. (1998) in their analysis of the relationship between *P. truncatus* larval survivorship and moisture content of maize, was used to describe the relationship between *P. truncatus* reproductive rate ( $R_m$ ) and moisture content of host materials at the time of infestation ( $m$ ):

$$R_m = a \times \exp \left[ -0.5 \times \left( \frac{(m - x)}{b} \right)^2 \right] \quad [1]$$

where  $a$ ,  $b$ , and  $x$  are fitted coefficients with the initial values of 5, 12, and 35, respectively, and  $x$  represents the optimum moisture content. Only rearing tests with confirmed reproductive rate were included in the regression analyses.

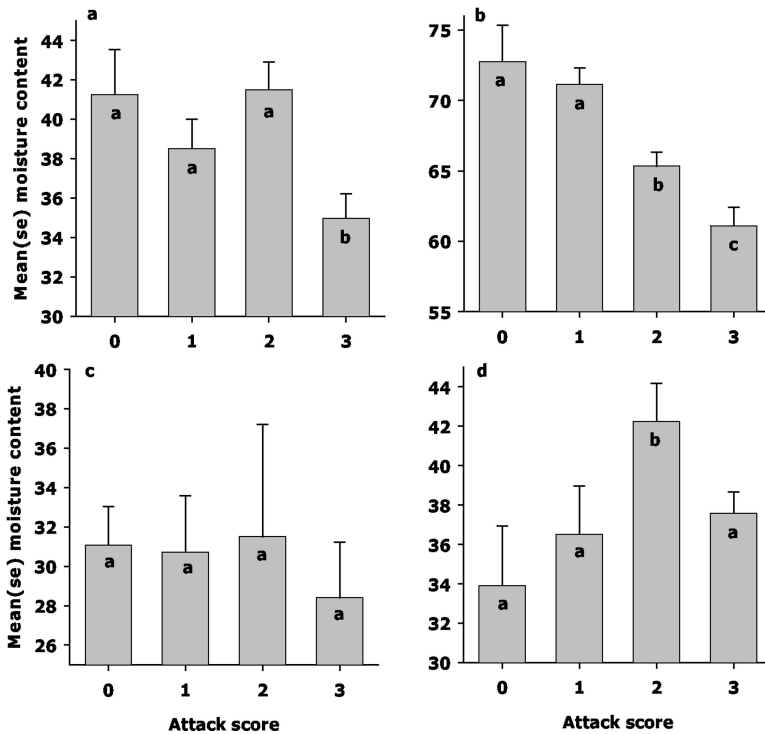


Fig. 1. Relationship between attack score of *P. truncatus* after 2 wk of rearing and moisture content of fresh branches of *C. pentandra* branches (a), *M. esculenta* (b), *F. exasperata* (c), and *D. regia* branches (d): 0, no entry holes; 1, one or two entry holes; 2, three to five entry holes; or 3, more than five entry holes. Different letters in bars represent significant differences in a PROC MIXED comparison with contrasts ( $\alpha = 0.05$ ), and number of replicates for each bar is presented in Table 1.

## Results

**Reproductive Rate of *P. truncatus* Strains.** There were significant differences in the reproductive rates of *P. truncatus* among the six different host materials that were tested with laboratory-raised and wild-caught *P. truncatus* ( $F_{5,89} = 284$ ;  $P < 0.001$ ), but there was no significant difference between the two *P. truncatus* strains ( $F_{1,89} = 1.89$ ;  $P = 0.07$ ), and the IITA strain was used for all further tests.

**Attack Score of Branches and Roots.** Of a total of 2,996 rearing tests conducted on branches (Tables 1 and 2), roots (Table 3), and seeds, the majority yielded either low or no attacks by *P. truncatus*. No entry holes were observed in all rearing tests with fresh branches from five tree species [girdled branches of *A. occidentale*, *Anogeissus leiocarpus* (DC.) Guill. et Perr. (Combrétaceae), *Dialium guineense* Willd. (Fabaceae), and *Khaya senegalensis* (Desr.) A. Juss. (Meliaceae) (Table 1)], dry branches from eight tree species (Table 2), and fresh roots from 12 tree species (Table 3). An attack score of three (more than five entry holes) was recorded in 18% of all tests on fresh branches of 11 tree species, on dry branches from four species, and on fresh roots from only three species. For most tree species, fresh branches were tested over a range of moisture contents, and a statistical comparison of means was for four of the host materials: for rearing

tests with fresh branches of *C. pentandra*, the moisture content associated with an attack score of three was significantly lower of rearing tests with lower attack scores (Fig. 1a). For *M. esculenta* (Fig. 1b), there was no significant difference in moisture content between rearing tests in which the attack score was 0 and 1, but higher attack scores were associated with progressively lower moisture contents. In the case of *D. regia*, both high and low attack scores were associated with low moisture content (Fig. 1c). There was no significant relationship between moisture content and attack scores for *F. exasperata* (Fig. 1d).

**Reproductive Rate on Potential Forest Hosts.** *P. truncatus* was able to reproduce on fresh branches from nine tree species (Table 4) with highest reproduction on branches of (in brackets the observed maximum reproductive rate): *D. regia* (8.25 $\times$ ), *C. pentandra* (3.90 $\times$ ), cassava stems (17.1 $\times$ ), and *F. exasperata* (3.10 $\times$ ). *P. truncatus* reproduction on dry branches was only observed on *F. exasperata* and girdled branches of *L. nigritana*, and the maximum reproductive rate on these branches were 0.80 and 0.20 $\times$ , respectively. Note that the highest reproductive rate on all branches was considerably lower than the average reproductive rate on whole maize kernels ( $n = 10$ , average = 21.9 $\times \pm 1.4$  SE). *P. truncatus* reproduced on roots from six of the tree species, with



Table 4. Reproduction rate of *P. truncatus* on branches and roots

Species	Substrate	Type	Mean (SE)	Reproductive rate			
				0	0–0.5	0.5–2.5	>2.5
<i>D. regia</i>	Branch	Fresh	1.68 (0.19)	88	20	28	47
<i>F. exasperata</i>	Root	Fresh	2.96 (0.74)	2	4	4	8
<i>M. esculenta</i>	Branch	Fresh	0.46 (0.18)	150	9	7	7
<i>F. capensis</i>	Root	Fresh	3.05 (0.68)	2	0	10	6
<i>F. exasperata</i>	Branch	Fresh	0.20 (0.05)	169	2	15	5
<i>Ceiba pentandra</i>	Branch	Fresh	0.14 (0.02)	430	75	41	4
Not included in regression analysis of moisture content and reproductive rate							
<i>L. nigritana</i> (Gird)	Branch	Dry	1.08 (0.40)	1	1	3	1
<i>F. exasperata</i>	Branch	Dry	0.30 (17)	14	0	3	1
<i>S. tragacantha</i>	Root	Fresh	0.42 (0.20)	6	2	4	0
<i>C. africana</i>	Branch	Fresh	0.11 (0.05)	22	7	1	0
<i>A. africana</i>	Root	Fresh	0.11 (0.06)	8	3	1	0
<i>F. xanthoxyloides</i>	Root	Fresh	0.04 (0.02)	9	3	0	0
<i>S. tragacantha</i>	Branch	Fresh	<0.01	91	2	0	0
<i>T. superba</i>	Root	Fresh	<0.01	10	2	0	0
<i>F. capensis</i>	Branch	Fresh	<0.01	104	1	0	1
<i>L. nigritana</i>	Branch	Fresh	<0.01	68	1	0	0
<i>T. superba</i>	Branch	Fresh	<0.01	80	1	0	0

Reproductive rate was defined as the number of offspring divided by the initial population of 20 unsexed *P. truncatus* individuals, and numbers in cells reflect the numbers of rearing tests in which the reproductive rate was within the given intervals. “(Gird)” after species name means that the branches had been girdled by cerambycids before collection in the forest.

the highest reproductive rate on *F. exasperata* (9.45×) and *F. capensis* (5.1×) (Table 4). For both *Ficus* species, *P. truncatus* reproduction was observed in all tests with an average reproductive rate of 3.0. The *P. truncatus* reproductive rate on *F. capensis* roots is noteworthy because negligible reproduction was observed on the branches. Conversely, *P. truncatus* did not reproduce on roots of *D. regia* or *C. pentandra* although reproduction did occur on the branches. No *P. truncatus* reproduction occurred on dry roots of *F. capensis* or *F. exasperata*. Six of the eight best-performing host materials were selected for evaluation of the relationship between moisture content and reproductive rate of *P. truncatus*, and there was a significant fit of equation 1 to all of them (Table 5). Girdled branches of *L. nigritana* and roots of *Sterculia tragacantha* Lindl. (Sterculiaceae) did well, with *P. truncatus* reproductive rate on 50 and 33% of the samples, respectively, scoring >2.5. However, the low number of branches of these species, due to their comparative rarity in the Lama forest, precluded their use in the moisture content analysis. Curves fit to data from fresh branches

from *D. regia*, fresh roots from *F. exasperata*, and *F. capensis* (Fig. 2) were bell-shaped with an optimal moisture content from 35 to 50% and optimal reproductive rates of ≈4.5, 8, and 6×, respectively. For fresh branches of *C. pentandra*, *F. exasperata*, and *M. esculenta*, we obtained significant curve fits (Table 5), but the coefficient *x* (optimal moisture content for reproduction) was negative and therefore has no biological meaning.

No reproduction of *P. truncatus* was observed on seeds of *A. africana*, *V. paradoxa*, or *E. guineensis*. In total, 191 rearing tests were conducted with teak seeds from four phenological classes, and *P. truncatus* reproduction was documented twice on seeds belonging to class 2: in one test a single late instar was found inside the teak seed and in another four adults and one larva were recovered in addition to the initial six adults. *P. truncatus* always attacked the soft mesocarp of teak seeds but rarely succeeded in penetrating the hard endocarp. No *P. truncatus* adults or other insects emerged from monthly field-collected teak seeds. Laboratory conditions were probably not optimal be-

Table 5. Regression analysis of the relationship between moisture content of fresh hosts and reproductive rate of *P. truncatus*

Species	Substrate	No.	Regression coefficients			df	F
			<i>a</i>	<i>x</i>	<i>b</i>		
<i>D. regia</i>	Branch	95	4.58	33.22	11.99	94	51.54***
<i>F. exasperata</i>	Root	16	8.05	49.40	5.57	15	16.62***
<i>M. esculenta</i>	Branch	24	366.10	−165.20	65.49	23	7.20**
<i>F. capensis</i>	Root	16	5.49	35.13	7.36	15	15.97***
<i>C. pentandra</i>	Branch	124	10.31	−2464.70	1062.90	123	42.97***
<i>F. exasperata</i>	Branch	23	32.61	−1439.20	598.90	22	20.57***

The relationship between moisture content and the reproductive rate for hosts which had been shown to be susceptible to *P. truncatus* (Table 4). “No.” refers to the number of rearing tests in which *P. truncatus* reproduction was obtained, and tests with no *P. truncatus* reproduction were excluded from the regression analyses. Reproductive rate was defined as the number of offspring divided by the initial population of 20 unsexed *P. truncatus* individuals after 2 mo of rearing, and it was compared with the moisture content at the beginning of each rearing test. The curve fit in equation 1 was used to examine the relationship between moisture content of fresh hosts and reproductive rate of *P. truncatus*.

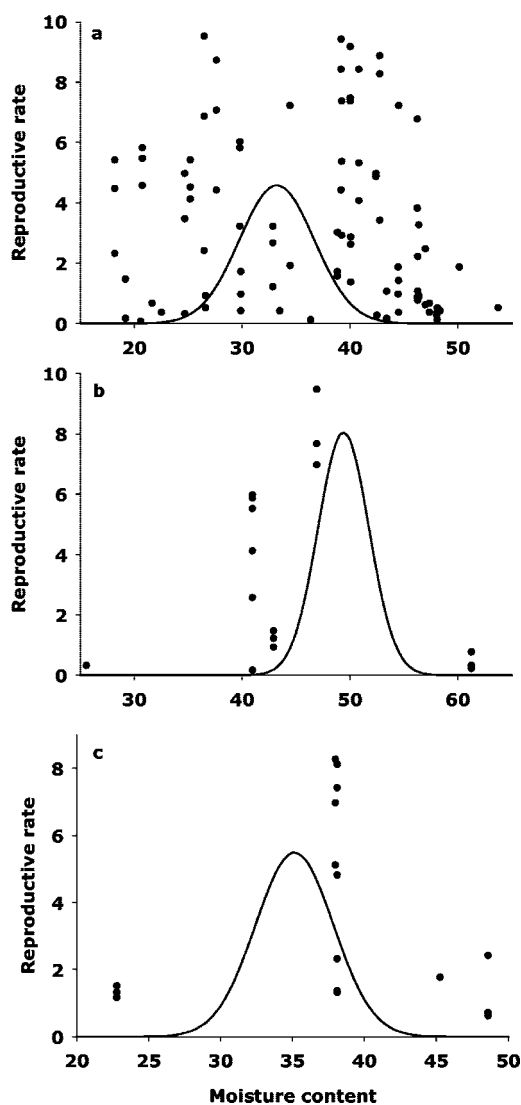


Fig. 2. Relationship between moisture content and reproductive rate of *P. truncatus* for: *D. regia* branches ( $n = 95$ ) (a), *F. exasperata* roots ( $n = 16$ ) (b), and *F. capensis* roots ( $n = 16$ ) (c). Points show results from all rearing tests with confirmed reproduction, and lines show the significant curve fits (Table 5).

cause many seeds were attacked by unidentified fungi during the 2 mo of rearing.

**Teak Seed Production.** Teak seed production was estimated to be 104.4 seeds per square meter per year in the teak plantations of the Lama forest. Teak seeds with holes in both the meso- and endocarp were frequently found on the forest floor, and these holes were similar in size to holes made by *P. truncatus* in the laboratory tests with teak seeds.

***P. truncatus* and the Soil Environment.** After studying the fairly high and consistent reproduction of *P. truncatus* on *Ficus* roots, we investigated how *P. truncatus* behaved when placed on top of soil in open jars.

No dead beetles were found after 48 h in any of the 20 tests, and 42 *P. truncatus* individuals were found circulating on the soil surface, 20 had flown, and 38 were found alive in the soil; of the latter 18 individuals had penetrated in the mesocarp of the buried teak seeds.

## Discussion

One of the most important factors in the survivorship and development of *P. truncatus* on maize is moisture content (Meikle et al. 1998). In this study, we found significant bell-shaped curve fits of moisture content to the reproductive rate of *P. truncatus* on fresh branches of *D. regia* and on fresh roots of *F. capensis* and *F. exasperata*, which suggests that the range of moisture contents of the host material was probably appropriate. However, in comparison with *P. truncatus* on maize, the minimum moisture content necessary for *P. truncatus* reproduction was very different than that observed by Bell and Watters (1982), and the strength of these relationships between moisture content and reproductive rate, which included only tests with successful reproduction, was much poorer than that observed by Meikle et al. (1998). In addition, we found no clear relationship between reproductive rate and moisture content for three other potential forest hosts (fresh branches of *M. esculenta*, *F. exasperata*, and *C. pentandra*; Table 5). It is therefore unlikely that moisture content alone explained the low *P. truncatus* reproductive rates on the examined host materials. Due to time and labor limitations many host parameters (e.g., nutritional value, age, abundance of allelochemicals) were not controlled and some may have played a critical role in *P. truncatus* reproductive success.

**Girdled Branches as a Resource.** Girdled branches are so far the only nonagricultural hosts in which *P. truncatus* adults and larvae have been found in the field. Based upon studies in Mexico, Ramírez-Martínez et al. (1994) concluded that the girdled branches could only serve as host for *P. truncatus* in the dry season, because the branches were too moist during the rainy season. In Kenya, Nang'ayo (1996) monitored cerambycid girdling on four savanna tree species, two unknown species of *Commiphora* [referred to by Nang'ayo (1996) as *C. riparia* and *C. abbreviata*], *Commiphora africana* (A. Rich.) Engl. (Anacardiaceae), and *Sterculia africana* (Lour.) Fiori (Sterculiaceae) for 20 mo and was unable to establish a clear link between branch girdling and seasonal *P. truncatus* flight activity. In Benin, Borgemeister et al. (1998) dissected two collections of girdled branches of *L. nigritana* from the Lama forest, and they showed that the beetle density was 0.9 ( $n = 63$  branches) and 2.6 ( $n = 40$  branches) *P. truncatus* individuals per branch. The mean reproductive rate of 1.08 in this study was consistent with the findings by Borgemeister et al. (1998). However, Borgemeister et al. (1998) also showed that the girdled branches of *L. nigritana* are attacked by 16 other beetle species, indicating that *P. truncatus* would have to contend with a considerable number of predators, parasitoids, and competitors.

**Nongirdled Branches and Roots as a Resource.** Nang'ayo (1996) conducted no-choice rearing tests in the laboratory and showed that the branches of many tree species found in the Kenyan savanna were acceptable for reproduction by *P. truncatus*, although the reproductive rate was inconsistent and generally low. Three tree species included in this study were also tested by Nang'ayo (1996) (average reproductive rate of five tests): *D. regia* (12.08), *C. africana* (2.08), and *A. occidentale* (0.54). In our study, we conducted 183 tests on fresh branches of *D. regia*, and 41% of these supported *P. truncatus* reproduction of 0.5 or greater. *P. truncatus* reproduction on *C. africana* was 0.5 or greater in 3% of the tests, whereas we obtained no *P. truncatus* reproduction in three tests on *A. occidentale*. In addition, *P. truncatus* reproduction of 0.5 or greater was obtained in 8% of tests on *C. pentandra*. Kossou (1992) conducted choice and no-choice experiments with branches from 10 tree species, and he obtained a reproductive rate of 0.18 per day on teak wood over a 45-d period. Teak branches collected monthly over 15 mo were offered to *P. truncatus* in 141 trials with no observed reproduction; indeed, *P. truncatus* seemed reluctant to even bore into teak branches. Fresh roots of *F. exasperata* and *F. capensis* proved highly acceptable to hosts because >66% of the tests with these hosts provided *P. truncatus* reproduction of 0.5 or greater.

**An Ecological Approach to the Evaluation of Potential Hosts.** The findings by Ramírez-Martínez et al. (1994), Nang'ayo (1996), and Borgemeister et al. (1998) concerning forest hosts of *P. truncatus* certainly underscore the necessity of treating *P. truncatus* as an insect with only secondary adaptation to the stored-product environment. However, the information might be more useful if it is placed in an ecological context by linking it to information on the abundance and spatial distribution of the observed or potential hosts. A crucial problem with no-choice rearing tests under laboratory conditions is that natural infestations by *P. truncatus* in nonagricultural hosts are very difficult to simulate under controlled laboratory conditions, so such rearing results are only meaningful when analyzed in an ecological context.

In the following, we use published studies, conducted in the Lama forest, on the spatial distribution of pheromone-baited trap catches *P. truncatus* (Nansen et al. 1999, 2002), the abundance and spatial

distribution of tree species (Nansen et al. 2001), the density of *P. truncatus* in girdled branches of *L. nigritana* (Borgemeister et al. 1998), and the rearing tests from this study to estimate *P. truncatus* populations from different potential forest hosts. Using this information, and a set of clearly stated assumptions, we attempted to make quantitative comparisons among hosts and determine their likely role in *P. truncatus* ecology. To generate the population estimates, we assumed that 1) In the comparatively closed environment of the forest, pheromone-baited trap catches of *P. truncatus* are positively associated with population density; 2) each trap has an effective range of 100 m [Farrell and Key (1992) recommended traps in sorghum, *Sorghum bicolor* (L.) Moench, fields to be placed no closer than 340 m to eliminate interactions] and samples ≈3 ha; and 3) immigration to and emigration from a trap zone are equal. Nansen et al. (2002) reported an average weekly trap catch in the Lama forest of 179.2 beetles, or ≈3,100 *P. truncatus* individuals per hectare per year. We used the vegetation study of the Lama forest by Nansen et al. (2001) to estimate the abundance of the different tree species. Borgemeister et al. (1998) collected girdled *L. nigritana* branches of <125 cm, so the reproductive rate from our rearing tests (based upon a total of 16 cm of host material) was multiplied by 7.8 to be directly comparable with the beetle density on girdled *L. nigritana* branches.

**Estimate of *P. truncatus* Population from Girdled Branches.** Nansen et al. (2001) showed that the average total tree density in the Lama forest was 1,136 trees per hectare and that the *L. nigritana* density represented 3.3% of that, or ≈37.5 trees per hectare. Assuming all the observed 3,100 *P. truncatus* per hectare originated from *L. nigritana*, then 82.7 *P. truncatus*, on average, emerged from each *L. nigritana* tree. From the mean reproductive rate of 1.1 observed in our rearing tests, we can estimate that ≈8.4 *P. truncatus* could have emerged from each branch, and the total number of branches per tree required to explain the trap catches would be ≈10 (Table 6). However, Borgemeister et al. (1998) observed an average of about two *P. truncatus* individuals produced per girdled branch in the field, in which case each *L. nigritana* tree would need to produce an average of 41.3 girdled branches per year. Although the annual branch production per tree was not measured, *L. nigritana* tend

Table 6. Population estimates on the basis of vegetation data, rearing results on hosts, and pheromone-baited trap catches

Species	Substrate	Density/ha	Beetles/tree	Reproductive rate/ branch or root (1.25 m)	No. of branches or roots
<i>F. capensis</i>	Root	25	124	23.8	5.2
<i>L. nigritana</i> (Gird)	Branch	37.5	82.7	8.4	9.8
<i>F. exasperata</i>	Root	6.8	454.5	23.1	19.7
<i>C. pentandra</i>	Branch	70.4	44	1.1	40.3
<i>F. exasperata</i>	Branch	6.8	454.5	1.6	291.4

Density/ha; mean density per hectare of trees was calculated on the basis of the vegetation study by Nansen et al. (2001). Reproductive rate, mean reproductive rate from four 4-cm pieces (16-cm) of host material (Table 4). Beetles/branch/root (1.25 m), reproductive rate was extrapolated into values for whole branches or roots of an average of 1.25 m. No. of branches/roots; number of branches or roots required to explain estimated pheromone-baited trap catches inside the Lama forest of 3,100 *P. truncatus* individuals per hectare (Nansen et al. 2002).



to be fairly small trees (usually <5 m in height) with a stem diameter rarely exceeding 20 cm, and it was seen as unlikely that even large trees of this species could annually produce more than five branches, particularly if the branches are harvested (girdled) every year. These two estimates show some of the challenges associated with interpretation laboratory rearing tests, and it is likely that the lower reproductive rate in the forest compared with the laboratory is at least partially explained by natural enemies and by competition, although further study is needed. In any case, Nansen et al. (2003) showed that pheromone-baited trap catches of *P. truncatus* in the Lama forest were comparatively low at sites with high densities of girdled and nongirdled *L. nigriflora*.

**Estimates of *P. truncatus* Population from Nongirdled Branches and from Roots.** The highest *P. truncatus* reproductive rate on branches was obtained on *D. regia*. However, this species is an ornamental tree that does not occur in the Lama forest and is rare in the vicinity of the forest. *P. truncatus* reproductive rate was 0.5 or greater in 10% of the cassava stems tested. Cassava is an important crop in the area, but it is not cultivated inside the Lama forest. In rearing tests, the two most acceptable fresh branches were *F. exasperata* and *C. pentandra*. Lacking information on natural infestations of *P. truncatus* in these branches, we used the results from the rearing tests to calculate population estimates on these hosts, as it was done for girdled *L. nigriflora* branches (see above). The estimated *P. truncatus* population (3,100 beetles per hectare) was divided by the mean density per hectare of trees to obtain the estimated mean number of *P. truncatus* individuals emerging from each tree. The mean reproductive rates from the rearing tests (four 4-cm pieces) were extrapolated into values for whole branches or roots of an average of 1.25 m, and the estimated mean number of *P. truncatus* individuals emerging from each tree was divided by the reproductive rate per branch to estimate the number of branches or roots required to explain the estimated *P. truncatus* population (Table 6). The calculations indicated that, for *F. exasperata*, each tree must, on average, have 291 infested branches per year to explain the pheromone-baited trap catches. However, if the same analysis and assumptions are applied to the tested root material, only an average of five 1.25-m roots per tree of *F. capensis* may explain the trap catches. These estimates should be considered very rough, but they suggest that fresh branches most likely can be dismissed as important for the *P. truncatus* ecology in the Lama forest and that the potential production from *Ficus* roots seems to justify further investigation as a potential forest hosts, on par with girdled branches of Anacardiaceae.

It may be that a given branch or root is acceptable for reproduction by *P. truncatus* over a long period of time and therefore the reproductive cycle is repeated one or more times, so a given girdled *L. nigriflora* branch may produce more individuals than a single sampling would indicate. However, the number of such cycles would need to be very large to explain the

discrepancy between observed *P. truncatus* trap catches and potential production from most branches and roots. This is unlikely, especially because such branches and roots are rapidly attacked by decaying wood insects, particularly termites.

According to Nansen et al. (2001), *F. exasperata*, *F. capensis*, and *L. nigriflora* generally occur in the same forest type, disturbed fallow, which is common in the Lama forest (Nansen 2000) but not spatially associated with the distribution of *P. truncatus* trap catches (Nansen et al. 2002). The lack of association between vegetation type and trap catches weakens the case for, but does not eliminate, these tree roots being important forest hosts. Some aspects of the root structure suggest that they could be easily exploited by *P. truncatus*. From preliminary excavations around trees, we found that *F. exasperata* has well-developed lateral roots close to the soil surface (<15 cm in depth) up to a meter from the stem, whereas the root structure of *F. capensis* is generally more vertical. That *P. truncatus* did not fly away during a 48-h time period but rather moved into and through the soil environment supports the argument that roots may be considered potential hosts. Evaluating roots as an important resource for *P. truncatus* would require surveys to estimate root mass and to find infested roots; these surveys were not conducted here. The potential of tree roots as a resource for *P. truncatus* needs further examination.

**Estimates of *P. truncatus* Population from Teak Seeds.** Observed annual teak seed production in the Lama forest multiplied by the rate of successful reproduction on teak seeds in rearing experiments provided a rough estimate of the potential importance of teak seeds as a host. If we assume that *P. truncatus* individuals only attack 1% of the teak seeds produced, that reproduction occurs on only 1% of those seeds (as was observed here in no-choice experiments), and that a seed is attacked only once with reproductive rate of two *P. truncatus* per seed, then the  $\approx 5,600$  ha of teak plantation around the Lama forest (Emrich et al. 1999), would produce  $\approx 1.2 \times 10^6$  *P. truncatus* individuals per hectare per year. This density is several magnitudes greater than that expected from branches of *L. nigriflora* and other hosts and could possibly account for the high numbers of *P. truncatus* observed in pheromone trap catches (occasionally >1000 per week) in the teak plantation in the Lama forest (Nansen et al. 2002, Nansen and Meikle 2003). A serious difficulty with this interpretation is that no *P. truncatus* were observed to emerge from seeds collected monthly on the ground in the Lama forest, although teak seeds with holes were frequently found in the Lama forest and these holes were very similar to the holes made by *P. truncatus* individuals during laboratory tests (Nansen and Meikle 2003). *P. truncatus* are known to bore into almost any material [including 35-mm plastic (Li 1988)], so it is possible that the seeds were bored by *P. truncatus*, although there are many wood-boring beetles of a similar size in the forest. The lack of observations of *P. truncatus* emergence might be partly explained by the lab rearing conditions, because we observed substantial fungal

growth on some teak seeds that may have interfered with the development of any *P. truncatus* within, and by the expected rarity of the attacked seeds. We collected a total of 1200 seeds and, assuming *P. truncatus* successfully attacked 0.01% of the seeds, which may be an upper estimate, and those seeds were randomly distributed over space and over the 10 mo, we would have had only one chance in nine of finding one. Furthermore, in their spatial and temporal analysis of the relationship between species composition and the size of *P. truncatus* pheromone-baited trap catches in the Lama forest, Nansen et al. (1999, 2002) found that 1) trap catches were highest where teak was the dominant vegetation type, and 2) the change in the spatial distribution pattern of pheromone trap catches over time suggested dispersal of *P. truncatus*, during the annual increase in flight activity, from areas where teak was abundant to other parts of the forest and nearby agricultural areas.

The idea that significant populations of bostrichids in general, and *P. truncatus* in particular, might be found in substrates other than branches or stored products is not new. Laboratory studies by Wright et al. (1990) showed that *Rhyzopertha dominica* (F.) (Coleoptera: Bostrichidae) can reproduce on acorns of *Quercus muehlenbergii* Eugelm. (Fagaceae), fruits of *Celtis occidentalis* L. (Ulmaceae), and *Symphoricarpos orbiculatus* Moench. (Caprifoliaceae), but infestations in the field could not be confirmed. Chittenden (1911) wrote that tubers and roots probably serve as the natural host for *P. truncatus*. Although Li (1988) found high *P. truncatus* reproduction on acorns of scarlet oak (*Quercus* spp.) (Fagaceae) in laboratory studies, field collections in oak forests in Honduras totalling ≈1000 acorns failed to confirm acorns as a host for *P. truncatus* (R. H. Markham, personal communication).

Certain aspects of the population estimates of production of *P. truncatus* from different forest resources should be considered very rough, such as the link between population size and trap catch. Although branches, roots and seeds of most of the important trees in the Lama Forest were included in this analysis, all tree components were neither tested nor available for all species, so this survey was not exhaustive. However, the population estimates indicate that future attempts to locate breeding *P. truncatus* individuals in forest environments should focus on sampling of host materials, such as roots and tree seeds, near or below the soil surface.

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